OBSERVATIONS UPON STENOSTOMUM ŒSOPHAGIUM

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The genus *Stenostomum* has been studied frequently since its first species was described by Ant. Dugès in 1828 as *Derostoma leucops*. There is considerable confusion in the records concerning the anatomy and life-history of the species of this genus. Our observations have to do with certain anatomical details and phenomena dealing with sexual propagation.

Material and Methods

The species *S. œsophagium* was described by Kepner and Carter in 1930, their description being based upon the first of the two clones employed by us. This first clone arose from an individual collected in September, 1929, and was maintained, in numerous lines, until July, 1930, when it died during the intense heat of the season. The second clone was established from a collection made in the last week of August, 1930. At the present writing, December, 1932, this clone is still running. Cultures have been maintained in wheat infusions,[1] little attention being paid to the hydrogen ion concentration. The range of pH for satisfactory cultures is from 5.6–7.6. Our most thrifty specimens have appeared in culture media that were on the acid side as low as pH 6.3.

The best material for sectioning was obtained by using hot (about 50° C.) Zenker's fluid. Iron hæmatoxylin, with eosin as a counterstain, was employed for the most part.

General Anatomy

The spindle-shaped body of this species measures about 1.5 mm. in length when no obvious fission plane is present. A specimen that has experienced inanition is colorless. A well-fed individual, on the other hand, has a yellow-brown tint due to the presence of absorbed food within the enteric epithelium. There are three external apertures: a ventral sub-terminal mouth; a ventral nephropore near the middle of the caudal region; and a dorsal, male gonopore that lies over the mouth. The body is covered with cilia.

[1] Four grains of wheat were boiled in 100 cc. of spring water and inoculated with bacteria, rotifers, and protozoa.

The epidermis bears numerous rhabdites (Fig. 1*B*, *r*) which lie in slender, parallel groups at the bases of the epidermal cells and expand distally to become almost uniformly distributed beneath the outer surface of the epidermis. In the fixed condition, the epidermis, from which the rhabdites have been discharged, shows deeply-staining chromatic lines (Fig. 2, *l*) that converge in each cell to form a common stem lying by the nucleus. However, these common stems show no morphological connection with the nuclei.

The alimentary canal consists of a mouth, pharynx, œsophagus, and enteron. These are all lined with a ciliated epithelium. The wall of the pharynx (Figs. 1 and 3, *ph*), is more muscular than that of the œsophagus. Furthermore, many unicellular glands (Fig. 3, *pg*) are loosely applied to the outer surface of the pharynx. These glands open into the lumen of the pharynx at its anterior end directly behind a small, dorsally directed diverticulum (Fig. 3, *d*). None of these glands crowd back over the œsophagus (Figs. 1 and 3, *œ*). Food-objects are delivered by the pharynx to the œsophagus, where they are held for a time before they are passed on to the enteron. A sphincter guards the passageway between these two regions of the alimentary tract. The enteron is an oval sac with a lining of ciliated endodermal cells. This epithelium (Figs. 1 and 3, *en*) in the living animal, under the usual vegetative conditions, presents a densely granular appearance. It is made up of tall, ciliated columnar cells (Fig. 4, *enc*), which may leave the epithelium and pass out into the pseudocœle. Figure 4 shows a cell

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Explanation of Figures, Plate I

FIG. 1. *A*. Dorsal aspect of a living specimen. *en*, enteron; *mgs*, male genital system; *oe*, œsophagus; *ov*, *ov'*, *ov''*, ovaries; *ph*, pharynx; *pn*, protonephridium. × 80. After Kepner and Carter (1930).

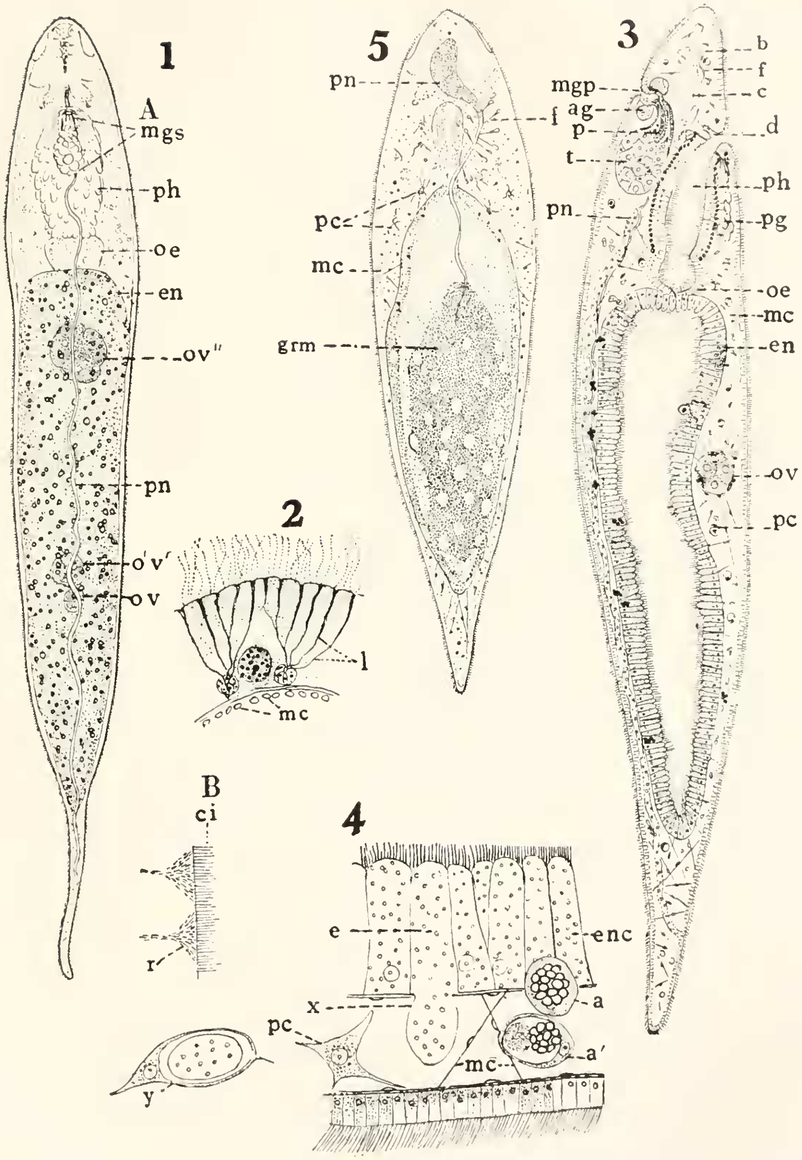
B. Region of living epidermis showing cilia (*ci*), and rhabdites (*r*).

FIG. 3. Sagittal section involving median plane. *ag*, accessory gland of male genital atrium; *b*, flexed part of protonephridium; *c*, neural commissure; *d*, dorsal diverticulum of pharynx; *f*, capillary region of protonephridium; *en*, enteron; *mgp*, male genital pore; *oe*, œsophagus; *ov*, ovary; *p*, penis; *pc*, phagocyte; *pg*, glands of pharynx; *ph*, pharynx; *pn*, main stem of protonephridium; *t*, testis. × 80.

FIG. 4. A region involving epidermis, pseudocœle, and endoderm of a living specimen as seen under water immersion objective. *a*, a wandering cell leaving epithelium of enteron, loaded with small bodies that it had taken up within the endoderm; *a'*, a similar cell that lies within the pseudocœle; *e*, endodermal cell leaving the epithelium, later its projecting end was sheared off; *enc*, endermal cell; *mc*, muscle cells; *pc*, phagocyte, which at *y* had ingested the fragment of endodermal cell that had been broken from *x*.

FIG. 5. Dorsal aspect of a specimen that had but recently deposited an egg. *f*, flame-cell; *grm*, granular material within the very thin-walled enteron; *mc*, muscle cells; *pc*, phagocytes; *pn*, region of protonephridium distended by granular inclusions. × 96.

PLATE I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that was leaving the epithelium while being observed under a water immersion objective. The shearing movements of the body-wall, however, tore the projecting part from the cell. This fragment of endodermal cell was soon ingested by the phagocyte (*pc*), which lay near, with the result shown in Fig. 4 at *y*. Between the ciliated cells of the enteron's epithelium other small cells may be found. We have seen these small cells appropriate refractive bodies, as they lay within the enteric epithelium, and then migrate from the wall of the enteron into the pseudocœle as shown in Fig. 4 at *a* and *a'*. This is taken up in greater detail by J. S. Carter (1933).

There are two bi-lobed cephalic ganglia, lying anterior to the mouth, with their larger anterior lobes in contact with the ciliated pits. An "eye-spot" is attached to each posterior lobe. The cephalic ganglia are connected by a transverse commissure (Fig. 3, *c*).

The protonephridium (Figs. 1 and 3, *pn*) is a conspicuous organ of the pseudocœle. This protonephridium consists of two regions, (1) a main stem and (2) a capillary-like portion. The main stem is the more conspicuous because of both its relative size and density. This entire organ lies in the mid-line, dorsal to the organs of the pseudocœle, except where it passes beneath the neural commissure. Anterior to this commissure, the protonephridium is bent upon itself. This deflection (Fig. 3, *b*) marks the boundary between the two regions of the protonephridium. The main stem has a thick cytoplasmic wall within which lie many nuclei, but in which no cell boundaries have been seen either in fixed or living material. The deflected part of the protonephridium appears to be a thin-walled syncytium. This capillary-like, posteriorly deflected region lies ventral to the main stem and is closely applied to it at irregular intervals. It receives scattered branches that have a similar structure. It is into this capillary-like portion of the protonephridium that the flame-cells (Figs. 3 and 5, *f*) empty. The anatomy of the

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Explanation of Figures, Plate II

Fig. 6. A phagocyte lying over a peripheral muscle cell (*m*). × 440.

Fig. 7. A median sagittal section of male reproductive system. *ag*, accessory gland; *mgp*, male gonopore; *p*, penis; *sp*, spermatids; *sv*, seminal vesicle; *t*, testis. × 416.

Fig. 8. Ventral aspect of a specimen that had but recently deposited an egg. *m*, mouth; *vo*, mesenchymal structure left in region in which egg had lain. × 80.

Fig. 9. A copulating pair in which the larger male is anchored to the anterior right side of the smaller one by the former's slender, colorless penis.

Fig. 10. Lateral aspect of mature female. Note reduced anterior or cephalic region. *e*, egg emerging as peristaltic waves travel towards it (indicated by arrows).

Fig. 11. A phagocyte that has ingested a muscle cell. *m*, muscle cell; *n*, nucleus of phagocyte. × 440.

PLATE II

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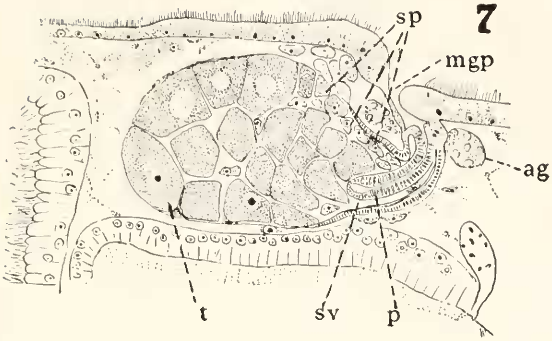

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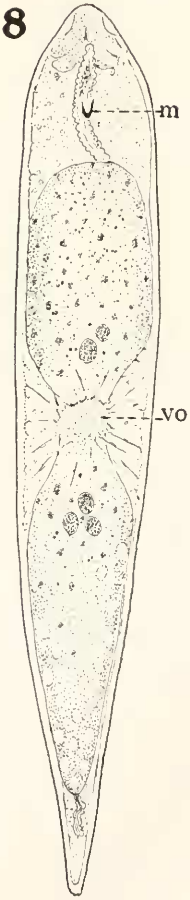

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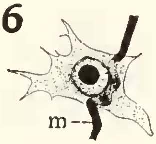

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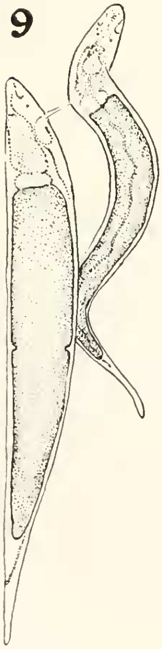

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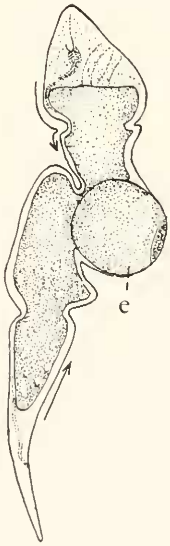

protonephridium of this *Stenostomum* is, therefore, similar to that described for *S. leucops* by Westblad (1923). Granular material has been observed frequently within the ciliated lumen of the thick-walled region but never within the lumen of the thin-walled region. This observation supports Reisinger's (1922, 1923) statement that the thick-walled region has an excretory function, while the thin-walled region has a filtering function.

Slender, non-striated, muscle-cells are associated with the body-wall, the walls of the enteron, œsophagus, and pharynx; while others (Figs. 3 and 5, *mc*) radiate from the alimentary canal to the body-wall.

Several types of leucocytes (Figs. 3, 4, and 5, *pc*) drift more or less passively within the pseudocœlomic fluid or crawl, amœba-like, over surfaces of muscle cells, between epithelial cells or to and into any other regions of the body. Figures 6 and 11 show two of these leucocytes. The gonads also lie within the pseudocœle.

Reproductive Organs

Vejdovsky (1880) was the first to have seen the male reproductive system, but he failed to recognize it as such and designated it the "ovale Drüse." Von Graff (1882) described only the female organs, while Sillimann (1885) saw the testis and expressed the opinion that the "ovale Drüse" of Vejdovsky was a sex organ. Voigt (1894) recognized both male and female gonads; while Keller (1894) gives a description of both the testis and the ovary. Landsberg (1887) records, "Hoden sah ich in derselben Kette, in der sich auch das Ovarium befand." Voigt (1894) likewise observed that *Stenostomum* was monœcious, while Sekera (1903) confirmed these observations. Von Graff (1913) states that "Die Geschlechtsorgane sind nur teilweise bekannt" (s. 18). Meixner (1924) records, "Hiezu sei vorläufig bemerkt, dass die dorsale Lage der männlichen Geschlechtsöffnung im Vorderkörper nur für etwa vier *Stenostomum-Arten* erwiesen ist" (s. 124). Sonneborn (1930) says, "Little is known concerning sexual reproduction in these organisms" (p. 59). Sabussow (1897) gave the most nearly complete description of the male reproductive system. He recognized five parts to this system in *S. leucops:* (1) a single testis; (2) a spheroidal seminal vesicle; (3) a tubular penis, lacking chitin, measuring "13 μ long and 11 μ breit"; (4) a penis-sheath; and (5) a small "antrum masculinum."

The male reproductive system of *S. œsophagium* corresponds to the description of that of *S. leucops* as given above by Sabussow (1897), except for the short tubular penis depicted and described by this author. We find that lying within the terminal duct, or neck, of the male organ is a highly muscular, tubular penis (Figs. 3 and 7, *p*). This occupies a position similar to that of the slime (*Schl* of Sabussow's Taf. 5, Fig. 1) which this author depicts and describes. We are therefore inclined to consider that Sabussow had mistaken the real penis of *S. leucops* for slime. The penis is an inverted tube capable of being everted. Its base, in the resting condition, gives the suggestion of a short tubular penis with a shallow penis-sheath. In reality it is clearly seen that in *S. œsophagium* there is a long tubular penis and that the penis-sheath shown in Sabussow's Fig. 1 is but a part of the genital antrum, the penis being housed, as a matter of fact, within the muscular seminal vesicle (Fig. 7, *sv*). In our Fig. 7 some spermatids are shown lying dorsal to the penis at *sp*.

Individuals which arise from eggs in the laboratory may become sexually mature, as males, in about three weeks. For example, an individual that emerged from the egg on December 16 was found to be sexually mature, as a male, on January 6. Sexually mature males may propagate asexually for many generations before female gonads appear.

There are no gonoducts associated with the female gonads. When oögonia are first seen in the living specimen, they lie beneath the ventral mid-line of the enteron within the pseudocœle. The growing primary oöcytes become enclosed in a loose, muscular tunic that is, in turn, supported by radiating non-striated myocytes. This rather indefinite aggregate of cells constitutes the ovary (Fig. 3, *ov*). We are not, as yet, in a position to state whether the oögonia are of mesenchymal or of endodermal origin. We are inclined to believe that they are diapeditic cells of the enteric epithelium. This subject will be taken up by one of us later.

Sekera (1903) observed that during the development of the "egg" four cells appear, one of which may function as the gamete and the remaining three may be used as yolk material. Our observations show that by the time the developing ovary becomes discernible in the living specimen, it is composed of two cells (Fig. 1, *ov*). After it has grown but a little more, the ovary contains four equal cells (Fig. 1, *ov′* and *ov″*). The gonad suggests the appearance of an embryo of four blastomeres. These cells, however, are not blastomeres. Despite the fact that there are thus always four cells in an advanced ovary, no ovary gives rise to more than one zygote. Only one of the four cells becomes the functional gamete, the other three having disappeared before egg-deposition. Both Sekera (1903) and Van Cleave (1929) indicate that at least the first cleavage of the zygote occurs before egg-deposition. We, however, are not in a position to confirm this.

A single ovary usually develops, but we have observed as many as seven ovaries develop and reach maturity in a given worm. The ovary usually lies in the anterior zoöid in specimens that present both a fission-plane and an ovary. However, specimens have been found frequently that displayed a well-defined fission-plane with an ovary in each zoöid. In these examples the anterior ovary was usually the more advanced (larger).

Copulation

There being no female gonoducts, copulation must be peculiar. We have observed two cases of copulation.

On one occasion, while a specimen that showed no discernible ovary was feeding, a second individual in a similar sexual condition (lacking a discernible ovary, but possessing a complete male genital system) approached the mass of food in such a way that its left anterior region lay near, but not in contact with the anterior end of the first animal. The penis of the first animal was everted with a high velocity so that its end pierced or adhered to the epidermis of the second male specimen (Fig. 9). Each animal, thereupon, made efforts to free itself as the two were held together by the translucent penis of the first animal. Their efforts eventually resulted in separation. The penis was then quickly drawn back into the seminal vesicle.

On another occasion we saw a similar series of phenomena differing only in that the point of contact of the penis with the second animal's body was at a different level from that involved in our first observation.

Voigt (1894) says, "Die männlichen Geschlechtsprodukte reifen erheblich früher als die weiblichen, so dass eine Selbstbefruchtung ausgeschlossen erscheint" (s. 747). Keller (1894) also says, "Die männliche Geschlechtsreife tritt erheblich früher auf, als die weibliche. Selbstbefruchtung ist somit nicht wohl anzunehmen" (s. 398). Sekera (1906) says, however, ". . . kommt es nach der Ausbildung der Dottermasse in den Keimzellen zur Selbstbefruchtung in der Weise, dass die Hodenfollikel platzen und reife Spermatozoen in der Leibeshöhle herumschwärmen, bis sie in die eine oder andre Keimzelle der einfachen Ovarien, welche nur aus 4 Keimzellen bestehen, hineindringen und zur Ausbildung eines Eichens mit dicker Eischale beitragen" (s. 142).

Our observations of copulation support the opinion of the first two authors. Furthermore, since copulation took place between individuals, each of which had no discernible ovary, it is suggested that the presence of foreign spermatozoa may be necessary for the development of latent oögonia. This suggestion is strengthened by the fact that we have no definite examples of isolated individuals becoming sexually mature as females; but our evidence in this connection is not sufficiently extensive to be convincing.

Egg-Deposition

The absence of female gonoducts has long attracted the attention of investigators. Voigt (1894) states, " Nach der Eiablage sterben die Tiere nicht ab, sondern sie fangen schon vor Beendigung derselben an, sich wieder durch Teilung fortzupflanzen " (s. 747). Von Graff (1913), Sekera (1926), and Van Cleave (1929) record that the egg is discharged by rupturing the epidermis, resulting in the death of the parent. Carter (1930) observed that while egg-deposition brings on a critical period, it is not necessarily fatal to the mother.

We have observed the details of egg-deposition. On January 25, 1931, we discovered a specimen that had an ovary surrounded by a translucent shell. The ovary's presence caused a conspicuous protuberance near the middle of the animal. The region in the immediate vicinity of the ovary displayed great and sustained muscular contraction. The regions anterior and posterior to the ovary presented peristalsis, the waves of which traveled towards the large ovary (Fig. 10). While we took turns watching this specimen (which was quiet, except for the peristalsis), one of us saw the epidermis open and slip back over the egg and close behind it as though the epidermis were an elastic membrane with a small pore through which the egg had passed by distending the pore. The pore closed after the egg's passage had been effected, leaving no wound in the body-wall. Neither cells nor plasma could be seen to have escaped with the egg. Within the pseudocœle lay the vestige of the muscular tunic of the ovary (Fig. 8, *vo*). We have made other similar observations of egg-deposition.

The period of incubation of the eggs, under laboratory conditions, varies greatly. Van Cleave (1929) obtained two incubation periods of twenty-five days each. We have had a period as short as fifteen days and one that extended well over a month. However, few eggs deposited under laboratory conditions developed.

The Influence of the Female Gonads upon the Parent

The ovary has a marked influence, both upon the life of the clone and that of the individual, for its presence influences both the fission-rate and the anatomy of the individuals. Van Cleave (1929) records that fission is inhibited by the ovary. Landsberg (1887), on the other hand, observed chains of zoöids in which the zoöids had female gonads. We have recorded frequent cases of fission in which the ovary lay in the anterior zoöid; so we may say that when an ovary appears anterior to an incipient fission-plane, this fission-plane is not inhibited in all cases; but a second fission-plane does not appear.

When, however, an ovary develops posterior to the fission-plane the usual events may not occur in the plane of division. The following is an example of such influence of a posterior ovary. January 24, 1931, we discovered an animal that was unusually long and had a fission-plane. Ordinarily a specimen with an advanced fission-plane measures about 3 to 4 mm. in length. This specimen, however, was 7 mm. long. The posterior zoöid had a conspicuous ovary. The anterior zoöid had a minute ovary that could be seen only with high magnification. The fission-plane's constriction indicated that it was an advanced one, but there were rudiments neither of ciliated pits, pharynx, cephalic ganglia, nor testis posterior to this plane of constriction. There was a small testes in the anterior zoöid. The enteron of the posterior zoöid housed within its wall refractive, oval bodies. On January 25 the specimen was indifferent to food. The posterior ovary had grown while the anterior one had not. On January 26 the posterior ovary had discharged its egg, the zoöid showing the depression within which the egg had been lying. The anterior ovary had not grown, but by January 27 the anterior ovary had enlarged. The posterior zoöid still showed the displacement of tissues that had been caused by the presence of the ovary, but no cephalic organs had developed. On January 28, the specimen had divided. At this time, the posterior zoöid lacked all cephalic organs. However, two weeks later this posterior zoöid had developed a pharynx, ciliated pits, and cephalic ganglia. This is but one of frequent similar examples that we have seen. Thus it appears that when an ovary is more advanced in the posterior zoöid, the formation of organs or differentiation of tissues in the region of the fission-plane is inhibited.

Sekera (1903) observed " Bald darauf beginnt auch der Pharynx zu degenerieren und das Individuum nimmt keine Nahrung auf, indem es durchsichtig und verkümmert zu werden pflegt " (s. 543).

We have found that the presence of a developing ovary makes an increased demand for material that must be supplied at the expense of the substance of the body as a whole. The leucocytes of the mesenchyme increase in number in the vicinity of the pharynx as the ovary grows. These become phagocytic and attack the radiating muscles of the pharynx and ingest them (Fig. 11). This phagocytosis eventually greatly reduces the size of the pharynx and œsophagus The testis completely disappears. The main stem or thick-walled region of the protonephridium is resorbed at irregular levels, sometimes leaving only an enlarged sack-like region (Fig. 5, *pn*) as a vestige of the main stem, and the capillary region bearing flame-cells (Fig. 5, *f*). This vestige becomes greatly distended and contains a dense mass of minutely crystalline material (Fig. 5, *pn*). With advanced phagocytosis, the wall of the enteron becomes quite thin and a mass of granular material (Fig. 5, *grm*) appears within its lumen. This material resembles that found within the distended anterior region of the main stem of the protonephridium at this time. It may be that with the reduction of the pharynx excreted materials can no longer escape by it and thus accumulate within the enteron as they do within the main stem of the protonephridium when it has been cut off from the exterior. The resorption of the anterior organs may be much more extensive than is indicated in Fig. 5. Frequently all of the cephalic structures have been resorbed.

The Turbellaria are usually considered to represent a phase in the phylogeny of the Annelida. That we should see extensive dedifferentiation associated with egg-formation in *Stenostomum* has some significance when the phenomenon known as epitoky in the annelids is considered; for it lends support to the theory that Annelida may have arisen from Turbellaria.

Some experiments were made to test the hypothesis that the reduction of the cephalic organs was necessary in order that material may be supplied to the egg. Specimens were taken that showed incipient ovaries. From these the "heads" were removed. In each case the wound healed, but no new "head" was formed until after the egg was laid. This supports van Cleave's (1929) observation that reconstitution does not occur in female specimens. However, the loss of cephalic tissue that would ordinarily be resorbed did not inhibit the growth of the ovary. In all cases the ovary reached maturity and an egg was laid. The growth of the ovary is therefore not dependent upon the resorption of the cephalic organs. It is suggested that the degree of resorption of cephalic organs, that takes place when the ovary is growing, is correlated with the relative age of the "head" involved. This is a line of observation that one of us plans to follow.

The Appearance of Male Gonads Dependent upon Extrinsic Conditions

Sekera's (1903) suggestion that the appearance of sex is determined by extrinsic factors is supported by our observations. Concerning *Stenostoma leucops*, he says "Aus meinen vieljährigen Beobachtungen, die ich schon vom Jahr 1885 an fort führe, kann ich mir erlauben zu behaupten, dass ein jeder Tümpel nach seiner physischen Beschaffenheit eine bestimmte Zeitdauer hat, in welcher alle Exemplare von *Stenostomum leucops*, *unicolor*, etc. geschlechtlich sich entwickeln. Damit hängt es auch zusammen, dass wir in den nassen Sommerzeiten, wo sich viel Wasser in den Tümpeln anhäuft, mit dem oben erwähnten ungünstigen Umstande für die Ausbildung der Geschlechtsorgane nicht zu rechnen haben" (s. 538).

Specimens have been taken from their natural habitat in May, June, July, August, and September during three years. We have found these to be sexually mature as males only during the last week of August and in September. The species appear to be carried through the winter by zygotes, for extensive collections made in early December and early March yielded no examples of this species.

In contrast to this we have maintained a clone that always presented sexually mature males and at irregular intervals sexually mature females through the year. In addition to this, we have raised sexually mature males from the egg within a period of a month.

It thus appears that certain extrinsic factors of the natural habitat arise in late August which determine the appearance of male gonads, while under laboratory conditions extrinsic factors are present which prompt the development of male gonads throughout the year. *S. œsophagium,* in being sexually mature as males under laboratory conditions, stands sharply in contrast with *S. tenuicauda*. Nuttycombe (1932) has maintained a clone of *S. tenuicauda* for over five years, during which time gonads have not appeared, although specimens collected from their natural habitat were sexually mature in the autumn.

Summary

The male gonad and gonopore lie dorsal to the anterior end of the pharynx. There is no female gonoduct.

The absence of a female gonoduct is correlated with a peculiar mode of copulation.

Egg-formation and egg-deposition bring about a crisis in the life of the individual which is not necessarily fatal. Extensive dedifferentiation and phagocytosis are associated with the development of the egg. After the egg has been laid, a new "head" is developed.

Development of male gonads, in this rhabdocœle, appears to be dependent upon extrinsic rather than intrinsic factors.

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